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Courtship behavior in European species of the genus *Pardosa* (Araneae, Lycosidae)

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Abstract. The study of courtship behavior provides a useful tool for identifying cryptic species due to the qualitative differences that can be observed in closely related species. Here, we present an overview of visual courtship displays of 26 European species of the genus *Pardosa* C.L. Koch 1847, including new quantitative and qualitative data. Thirty-five recurring courtship elements are described and illustrated by means of drawings, photos and videos (available online). In general terms, complex movements of the palps, the first pair of legs and the abdomen characterize courtship displays in the genus *Pardosa*. The most complex movements are performed by the palps, while legs and abdomen mainly oscillate in the air or vibrate on the substrate. We noticed a high level of complexity in almost all of the species, both in terms of sensory modes involved and number of courtship elements composing the displays. No apparent relationships emerged when considering ethological similarities among species, attesting to the relative independence between morphological and ethological characters.

Keywords: Displays, sexual communication, visual signaling behavior, wolf spiders

The lycosid genus *Pardosa* C.L. Koch 1847 is one of the largest spider genera in the world; Platnick (2012) lists more than 500 species, with about 60 valid species occurring in Europe. *Pardosa* spiders are diurnal wandering predators occurring in a variety of environments, but predominantly in open habitats. Several species have been placed in phenetic species groups based on similarities in the copulatory organs (e.g., Zyuzin 1979; Almquist 2005). Morphological characters, especially in females may overlap between species (Den Hollander & Dijkstra 1974), and it can be difficult to find distinct criteria for species identification (Vlijm & Dijkstra 1966; Töpfer-Hofmann et al. 2000). On the other hand, courtship displays, which are characterized by redundant and stereotyped movements, are species-specific and are considered diagnostic for species identification (Den Hollander & Dijkstra 1974).

Courtship behavior plays an important role in the pre-mating isolation mechanism between species. Since species may occur in syntopy or, at least, can be found in neighboring habitats and/or in the same season, ecological or phenological isolation seems in many cases to be insignificant. Under these circumstances, courtship behavior, in association with semi-ochemicals, may be regarded as an important barrier to prevent hybridization among *Pardosa* species (Töpfer-Hofmann et al. 2000).

According to Land (1985) and Rovner (1996), wolf spiders possess good image resolution but lack color perception. The male usually performs visual courtship display using complex movements of palps, forelegs and abdomen (Stratton 1985). In addition, males of some species have epigamic characters like divergent hairiness, deviant pigmentation of the first pair of legs and palps or a combination of these features (Kronestedt 1979a; Stratton 1985; Mc Clintock & Uetz 1996; Scheffer et al. 1996; Hebets & Uetz 1999, 2000; Taylor et al. 2005; Framenau & Hebets 2007). Moreover, communication by percussion, stridulation, and vibration of body parts is also well documented in wolf spiders (Rovner 1967, 1975; Buckle 1972; Kronestedt 1973, 1990, 1996; Stratton & Uetz 1981, 1983), with regard to both substrate-borne and air-borne vibrations. Chemical communication generally involves contact or airborne sexual pheromones and mediates different kinds of interactions (Rovner 1968; Tietjen 1979a, b; Stratton & Uetz 1981; Tietjen & Rovner 1982; Stratton 1985; Kronestedt 1986; Uetz 2000; Barth 2002; Uetz & Roberts 2002; Roberts & Uetz 2004). Contact pheromones are associated with female draglines (Hedgekar & Dondale 1969) and are detected by chemosensitive hairs in the male (Foelix & Chu-Wang 1973; Kronestedt 1979b).

Despite the potential in using courtship displays for distinguishing closely related species of the genus *Pardosa*, literature about European species is rather scarce (Den Hollander & Dijkstra 1974; Töpfer-Hofmann et al. 2000; Kronestedt 2007; Chiarle & Isaia 2013). With regard to North American species of *Pardosa*, studies have focused on *Pardosa falcifera* F.O.P.-Cambridge 1902 and *P. zionis* Chamberlin & Ivie 1942 (Vogel 1970) and *P. dromaea* (Thorell 1878) and *P. groenlandica* Thorell 1872) (Dondale & Redner 1990; Dondale 1999). In Japan, Suwa (1980, 1984) and Tanaka & Suwa (1986) studied the ethological differences among closely related species in the *P. laura* Karsch 1879 complex.

In view of the lack of ethological research on the genus *Pardosa,* in this paper we hope to contribute to the body of knowledge on this genus of wolf spiders, emphasizing its potential as a good model for studies on sexual communication. More specifically, the aims of this study are 1) to gather available information on the courtship displays of the European species of the genus *Pardosa*, integrating them with new observations; 2) to provide a detailed list and a description of the courtship elements (sensu Lehner 1998)

Table 1.—Sequences of courtship elements (see text for abbreviations) and previous published descriptions considered in this work. Courtship elements are grouped in the same row when they occur simultaneously.

Species	Courtship Elements Sequence	Previous courtship description
P. amentata	P_SE + A_TW P_Q + L_Q + A_Q	Locket (1923), Bristowe & Locket (1926), Schmidt (1957), Bristowe (1958), Vlijm et al. (1963), Vlijm & Dijkstra (1966), Vlijm et al. (1970), Cordes (1995)
P. bifasciata	P_W + L_WA B_H + L_WH + P_Q	none
P. schenkeli	P_P P_P + B_B + A_TA + L_WH	Kronestedt (2005)
P. lugubris	B_P P_TC + L_LS + A_TW	Vlček (1995: species A), Töpfer-Hofmann et al. (2000)
P. saltans	L_LS + P_TC + A_TW L_P + P_SRL + A_TW P_TRL B_E	Bristowe (1929: sub *Lycosa lugubris*); Vlijm & Dijkstra (1966: sub *P. lugubris*), Vlček (1995: species B), Töpfer-Hofmann et al. (2000)
P. agrestis	P_LWJ + L_O + A_TW A_TW + L_Q	Kronestedt (1979a)
P. agricola	P_W + L_O + A_TW	Kronestedt (1979a)
P. blanda	P_Q + A_Q B_H + L_WH P_UDJ + L_T + A_TA A_TW + P_W	none
P. mixta	B_SW L_R P_ARJ + A_TW L_WH + P_Q + A_TA	none
P. monticola	A_TW P_RL	Kronestedt (1979a)
P. palustris	B_SW + P_W + A_TW	Kronestedt (1979a)
P. purbeckensis	P_SWR + L_R P_SWR + L_O + A_TW	Bristowe (1929), Kronestedt (1979a)
P. torrentum	A_TW A_TA B_SW + L_O + P_UDJ	none
P. nigra	P_C + L_R B_H + L_WH	none
P. nigriceps	P_CC + L_Q + A_TW	Locket (1923), Bristowe & Locket (1926), Bristowe (1958), Vlijm & Dijkstra (1966)
P. hortensis	P_SC + L_Q + A_TW	Vlijm & Dijkstra (1966)
P. proxima	L_R + P_W + A_TW B_H + L_T + P_CR + A_TW P_CR	Den Hollander & Dijkstra (1974), Chiarle & Isaia 2013
P. vlijmi	B_B B_H + A_TW + P_CR + A_TA P_CR	Den Hollander & Dijkstra (1974), Chiarle & Isaia 2013
P. pullata	B_J	Bristowe & Locket (1926); Vlijm & Borsje (1966); Hallander (1967); Den Hollander (1971); Den Hollander et al. (1973); Kronestedt (1979a, 2007)
P. pyrenaica	P_W + B_J	Kronestedt (2007)
P. fulvipes	P_RL + A_TW L_WA + A_TW	Kronestedt (1979a)
P. prativaga	A_TA + P_CR P_Q A_TA + P_CR + P_Q B_H + A_TA + P_CR B_R B_E	Den Hollander et al. (1973), Kronestedt (1979a)
P. riparia	B_P P_W + A_TW	Kronestedt (1979a)
P. sphagnicola	A_TA + P_Q B_H + A_TA + L_T + P_CR B_R + A_TA	Den Hollander et al. (1971: sub *P. prativaga fulvipes*, 1973), Kronestedt (1979a)

Table 1.—Continued.

Species	Courtship Elements Sequence	Previous courtship description
P. wagleri	P_LJ + A_Q + A_TA B_P + L_WH + P_LJ + A_Q + A_TA P_RL	Chiarle et al. (2010)
P. saturatior	P_Q + A_Q + A_TA B_P + L_WH + P_Q + A_Q + A_TA P_RL	Chiarle et al. (2010)

recurring in *Pardosa*'s displays, with a goal of categorizing behavioral diversity in this genus; 3) to describe unknown courtship behaviors and add supplementary details to previous descriptions and 4) to compare different behaviors by focusing on similarities and differences among species.

FIELD COLLECTION AND MAINTENANCE

At the beginning of each paragraph describing courtship behaviors, we provide information on the material and number of observed courting males. We (AC, MI) collected the spiders in the field as adults or sub-adults and kept them in the laboratory, housed individually in cylindrical plastic containers (6 cm diameter, 2.5 cm high). Individuals were fed with two or three *Drosophila melanogaster* per week and provided access to a hydrated piece of cotton for water and humidity. We maintained spiders at 22 ± 1°C with a 10:14 h light:dark photoperiod. At the conclusion of each observation, spiders were preserved in ethanol for further molecular analysis. Voucher specimens are stored at the Museo Regionale di Scienze Naturali of Turin (Italy) (MRSN), at the Entomology Department of the Royal Belgian Institute of Natural Science in Brussels (Belgium) (RBINS) and at the Department of Life Sciences and Systems Biology, University of Turin (Italy) (DBIOS). Video samples of courtship display are stored at AC's personal website (www.ragnolupo.com) and are available on the Internet.

PUBLISHED DATA AND OTHER OBSERVATIONS

In an effort to provide a thorough history of the literature giving descriptions of courtship behavior of the 26 European species of *Pardosa*, we have included all of these speeies in our review. Most of the works were published between 1957 and 1979 (Table 1) and in only a few cases have these researchers presented and discussed quantitative data. In contrast, several recent descriptions are exhaustive and offer a comprehensive characterization of species' behaviors. In particular, this is the case with *Pardosa wagleri* (Hahn 1822) and *P. saturatior* Simon 1937 (Chiarle et al. 2010), *P. lugubris* (Walckenaer 1802), *P. saltans* Töpfer-Hofmann 2000, *P. pertinax* von Helversen 2000, *P. alacris* (C.L. Koch 1833) and *P. baehrorum* Kronestedt 1999 (Töpfer-Hofmann et al. 2000), *P. pullata* (Clerek 1757), *P. pyrenaica* Kronestedt 2007 (Kronestedt 2007), *P. proxima* (C.L. Koch 1847) and *P. vlijmi* Den Hollander & Dijkstra 1974 (Chiarle & Isaia, 2013).

Moreover, Kronestedt (1979a, 2005) published descriptions of the displays of *P. agricola* (Thorell 1856), *P. fulvipes* (Collett 1876), *P. monticola* (Clerck 1757), *P. palustris* (Linnaeus 1758), *P. agrestis purbeckensis* F.O.P.-Cambridge 1895, *P. riparia* (C.L. Koch 1833), *P. schenkeli* Lessert 1904, *P. sphagnicola* (Dahl 1908) and *P. prativaga* (L. Koch 1870) in local journals (in Swedish), for which we provide revised and improved descriptions gathered from the original super-8 films. In these cases, TK used a Beaulieu 4008 ZM super-8 camera provided with an Angénieux Macro-Zoom 1.9/8–64 mm lens. Spiders were collected as sub-adults or adults, kept individually in plastie containers with access to water and fed irregularly with *Drosophila melanogaster*. TK observed the spiders' behavior in a round plastic jar with the bottom (diameter 7 cm) covered with plastic foam. A segment of the jar was cut off and covered with a glass plate through which spiders were filmed and still-photographed using fiber optic illumination as a light source.

Regarding these observations, we provide the re-description of the basic courtship elements characterizing the average behavior of each species. When possible, we add quantitative data such as mean duration and standard deviation of courtship elements (given in seconds). Moreover, we provide sound recordings obtained by TK on *Pardosa schenkeli*, *P. prativaga* and *P. sphagnicola*. Sounds were recorded with a UHER 4200 tape reeorder from spiders performing courtship displays on a cardboard substrate in the observation jar. Data were analyzed using an audio program (Audacity).

Materials used in TK's studies are stored at the Swedish Museum of Natural History in Stockholm (Sweden) (NHRS).

NEW OBSERVATIONS AND RECORDING

Based on the observations of field-collected specimens, we provide new descriptions of the courtship behaviors of *P. bifasciata* (C.L. Koch 1834), *P. blanda* (C.L. Koch 1833), *P. mixta* (Kulczynski 1887), *P. nigra* (C.L. Koeh 1834) and *P. torrentum* Simon 1876. Moreover, on the basis of our new unpublished observations, we add new information about the courtship behavior of *P. agrestis* (Westring 1861), *P. amentata* (Clerck 1757), *P. hortensis* (Thorell 1872), *P. nigriceps* (Thorell 1856), *P. prativaga* (L. Koch 1870).

In order to obtain new descriptions or improve previous ones, AC and MI observed and recorded the male and the female in a glass arena (20 cm diameter, 5 cm high) on a sheet of absorbent paper to optimize the transmission of vibrations and the persistence of chemical traces (Rypstra et al. 2003; Chiarle et al. 2010). We used a white neon lamp as light source. We introduced the female into the arena for 15 min, in order to spread chemical traces and silk on the absorbent surface. We then placed the male in the arena and recorded its behavior for one hour, with two Canon HV30 cameras at 50i recording speed and then acquired with Adobe Premiere Pro CS3 (Adobe Systems Incorporated) at 1480×900 resolution. At the end of each trial, we cleaned the arena with paper and 75% ethanol in order to remove chemicals and silk cues. We provide the description of the courtships, including the basic

elements characterizing the behaviors, together with their frequency and duration (mean ± SD).

DESCRIPTION OF COURTSHIP ELEMENTS

Given the lack of comprehensive work on *Pardosa* courtship behavior, we provide a detailed list of the recurring courtship elements (*sensu* Lehner 1998) that we observed. Terminology is in most cases original, or inspired by previous work on *Schizocosa*.

For each part of the body involved in the behavior, we describe the basic courtship elements (CEs) recurring in the behaviors (Table 1); namely 17 elements for the palps, eight elements for the forelegs, three elements for the abdomen and seven elements for the whole body. Each CE is encoded by an alphabetical acronym starting with "P" if the behavior is related to palps, "L" for forelegs, "A" for the movement of the abdomen, and "B" in the case of general movement of the body. The second part of the code relates to the name of the CE (for example: P_SE = palpal semaphoring).

In order to help the reader with the visualization, the main CEs are illustrated in Figs. 1–16 for the palps, Figs.17–23 for the legs, Figs. 24–26 for the abdomen and Figs. 27–29 for the general body movements. Courtship elements are listed and described in the next section (in order of appearance within each category).

1) Palps

P_SE, *semaphoring* (Fig. 1): the male raises one palp above the eyes, then moves it forward and sideways with a quick movement of the trochanter-femur and patella-tibia joints. The cymbium is stretched upward at an angle of about 45° to the substrate. The male then raises the other palp, keeping it under the line of the eyes and moves it forward and laterally. The tip of the cymbium points forward and downward. The palps are then carried back to the starting position and stretched out. The whole movement starts again with the opposite palp.

P_Q, *quivering* (Fig. 2): a continuous fast movement of the palps, which are moved up and down along the vertical axis, involving the trochanter-femur and the patella-tibia joints, with the tip of the cymbium pointing downward.

P_W, *waving* (Fig. 3): the male slowly raises the palps and lowers them alternately with a vertical movement, involving the trochanter-femur and the patella-tibia joints. The cymbium points downward and at the end of the rotation is brought parallel to the substrate below the body. A slight tremble occurs during the whole process of waving.

P_P, *pointing* (Fig. 4): the palps are bent, forming a right angle between the tibia and femur. Then the male quickly stretches them in synchrony at the patella-tibia joint and maintains them parallel to the substrate, bringing them back quickly to the starting position, tips pointing down. The movement is repeated several times. Both palps may also be raised higher, involving the trochanter-femoral junction, but they never reach the height of the cephalothorax.

P_TC, *tip cycling* (Fig. 5): from a rather high posture, the male moves the palps circularly, from the left to the right, tips pointing outwards.

P_SRL, *slow raising-lowering* (Fig. 6): from a rather high posture, the male raises the palps and stretches them out alternately, with slow movements involving the patella-tibia junction.

P_TRL, *two-steps raising-lowering* (Fig. 7): raising of the palps in two-steps: at first the male raises the palps to the eye line (cymbium and tibia at right angle), then stretches them up. After the upright motion, the males lower the palps in synchrony.

P_LWJ, *lateral waving jerk* (Fig. 8): the male lifts one of the two palps with rapid jerky movements involving the patella-tibia junction. Within each movement, the cymbium points upward and forward. When the tibia is stretched up over the eyes, and the palp reaches maximum height, the male lowers the palp down rapidly. The cymbium points forward and then downward. At the end of the lowering process, movement is transferred to the other palp, which starts the in the same way. The palp that is not lifted is kept stationary or moved at the patella-tibia junction, in synchrony with the other palp. In some cases, the male lifts the two palps together.

P_UDJ, *up-and-down jerk* (Fig. 9): the male raises and lowers the palps along the vertical axis, involving primarily the trochanter-femur joints, bearing the cymbium slightly toward the body. During this movement, the palps are maintained in a slightly oblique position with the tip touching the substrate.

P_ARJ, *alternate raising jerk* (Fig. 10): the male lifts the palps alternately, in two or three steps (the movement can also be performed by one single palp). First they are stretched forward, oblique and kept in line with the eyes, involving the trochanter-femur and patella-tibia joints, then raised alternately over the cephalothorax, involving the trochanter-femur joints.

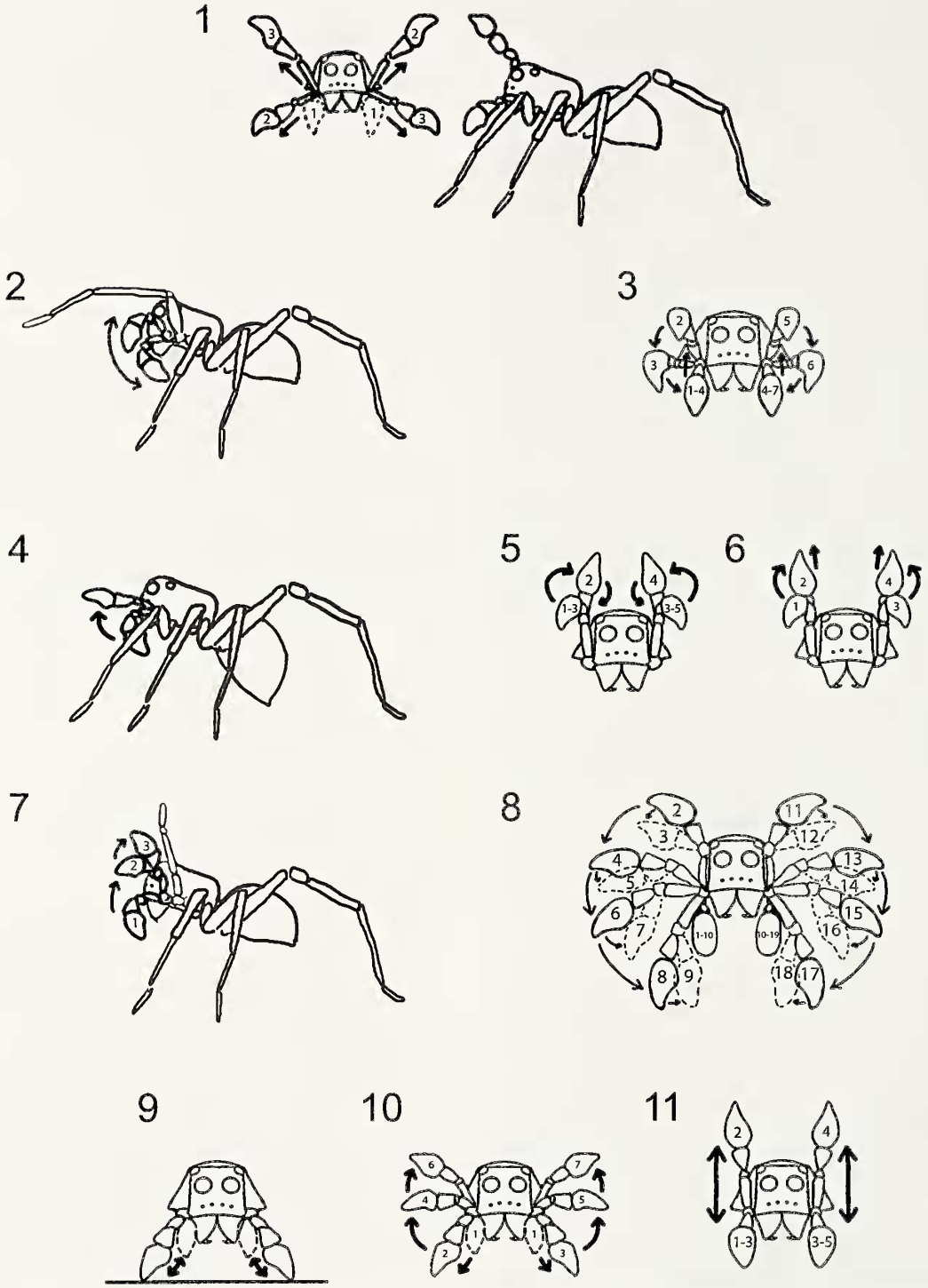
P_RL, *raising-lowering* (Fig. 11): the male raises one palp and quickly stretches it upward and forward, involving the trochanter-femur and patella-tibia joints. Then he lowers it, and brings it rapidly back to the starting position. This movement is repeated by the other palp or, less frequently, by the same palp.

P_SWR, *step-wise raising* (Fig. 12): the male raises the palps together in two or three steps. At first the palps are stretched forward in line with the eyes, involving the trochanter-femur and patella-tibia joints, and then they are raised over the cephalothorax involving the trochanter-femur joint. The male then often keeps the palps in the raised position, directed obliquely upwards. After that, the male slowly lowers both palps along the vertical axis with their tips directed downwards.

P_C, *circling* (Fig. 13): the male draws an ellipse with the two palps. The palps form a right angle between femur and tibia and move almost simultaneously. More precisely, the male raises the palps and allows their position to widen outwards slightly, then lowers them inwardly until they almost touch each other. The cymbia pointing downwards. This movement can be repeated several times.

P_CC, *continuous cycling* (Fig. 14): same as P_SC but without steps (palps are moved continuously).

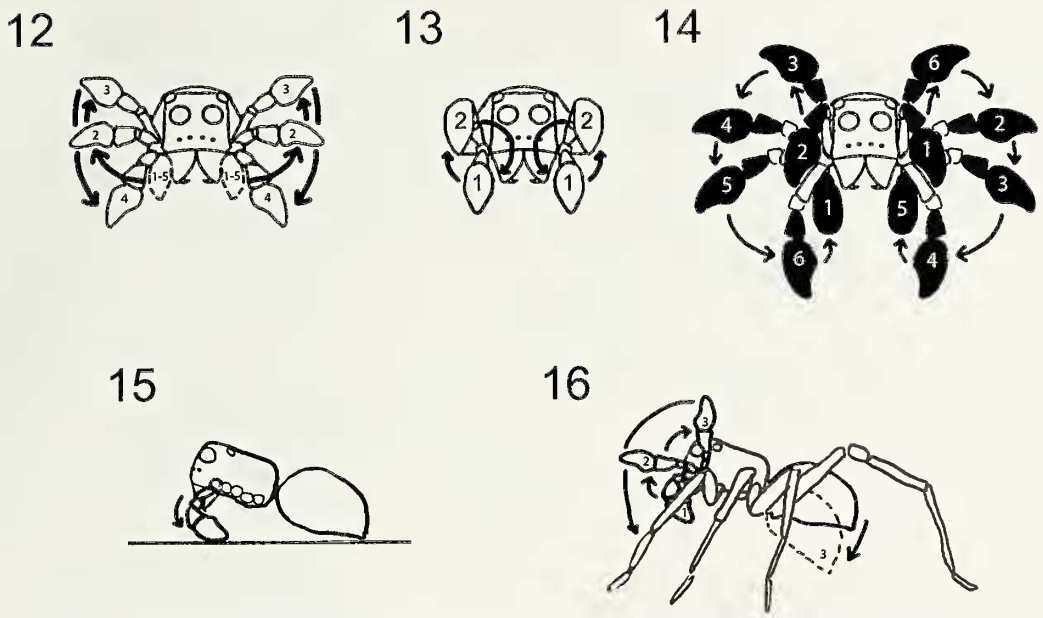
P_SC, *step cycling* (Fig. 14): the male raises one palp, tip pointing up (the movement involves trochanter-femur,



Figures 1–11.—Courtship elements in *Pardosa* species (palps). 1. Semaphoring (P_SE); 2. Quivering (P_Q); 3. Waving (P_W); 4. Pointing (P_P); 5. Tip cycling (P_TC); 6. Slow raising-lowering (P_SRL); 7. Two-steps raising-lowering (P_TRL); 8. Lateral waving jerk (P_LWJ); 9. Up and down jerk (P_UDJ); 10. Alternate raising jerk (P_ARJ); 11. Raising-lowering (P_RL). See text for abbreviations.

patella-tibia and tibia-tarsus joints). Then the same palp is lowered in 3–4 steps, performing lateral movements. During this movement, the tip of the palp draws half-circles until it returns to the resting position. This movement is repeated by both palps alternately or, in some cases, together. If one of the palps is not involved in the rotation, it remains still. During each step, the cymbium gently oscillates two or three times at the patella-tibia and tibia-tarsus joints.

P_CR, *cymbium rubbing* (Fig. 15): the palps are rubbed against the substrate with an active movement at the patella-tibia junction. The movement is mainly a consequence of the movement body (cymbium kept at ground level, rubbing on the substrate). Femur and tibia are kept at right angle.



Figures 12–16.—Courtship elements in *Pardosa* species (palps). 12. Step-wise raising jerk (P_SWR); 13. Circling (P_C); 14. Continuous\step cycling (P_CC, P_SC); 15. Cymbium rubbing (P_CR); 16. Low jerk (P_LJ). See text for abbreviations.

P_LJ, *low jerk* (Fig. 16): both palps are raised (bent at the coxa-femur and patella-tibia joints) and then lowered together, ending in a jerky, trembling movement.

2) Legs

L_WH, *whipping* (Fig. 17): the male raises the first pair of legs and stretches them until legs are almost perpendicular to the substrate. Immediately afterward, the legs violently hit the substrate or the female, if she is very close.

L_LS, *lateral stretching* (Fig. 18): the male stretches both forelegs laterally, upwards and outwards, in front of the female.

L_P, *pumping* (Fig. 18): the male stretches his legs in front of the female (L_LS) and then moves them slightly up and down. The movement involves the whole legs.

L_O, *oscillation* (Fig. 19): the male raises the first pair of legs, maintaining the femur almost perpendicular to the substrate (bent at the tibia junction). Tibia, metatarsus and tarsus are moved along the vertical axis with rapid small oscillations.

L_Q, *quivering* (Fig. 20): while moving toward the female, the male vibrates one or both front legs. The vibration may occur in contact with the substrate.

L_T, *tapping* (Fig. 21): the male raises the first pair of legs. Then, with a small vertical movement at the trochanter-femur junction, legs are lowered, hitting the substrate (tarsus kept approximately perpendicular).

L_WA, *waving* (Fig. 22): the male raises one foreleg at the trochanter-femur junction. During this movement, tibia, metatarsus and tarsus are stretched forward, parallel to the substrate. Subsequently, the foreleg is lowered until it touches the substrate. The movement can be repeated by the same foreleg or by the other one.

L_R, *raising* (Fig. 23): the male lifts the first pair of legs along the vertical axis, keeping the femur perpendicular to the substrate and the tibia perpendicular to the femur. Tibia, metatarsus and tarsus are stretched on the same line, parallel to the substrate. Forelegs can also be stretched with all segments perpendicular to the substrate.

3) Abdomen

A_TW, *twitching* (Fig. 24): a rapid vertical movement of the abdomen, which is kept parallel to the substrate, but not in contact with it. This CE can occur occasionally.

A_Q, *quivering* (Fig. 25): a series of fast movements of the abdomen, which is moved up and down along the vertical axis, parallel to the substrate, without touching it.

A_TA, *tapping* (Fig. 26): the abdomen is vigorously swung along the vertical axis, striking the substrate.

4) Body movement

B_SW, *sideways waving* (Fig. 27): the entire body moves slowly and rhythmically to the right and to the left. The waving involves the second, third and fourth pair of legs.

B_H, *hopping* (Figs. 28, 29): a series of generally jerky movements toward the female in the form of rapid jumps or short runs. The entire body often hits the substrate.

B_J, *jumping*: the male jumps onto the female in a single jump.

B_B, *bouncing*: the male quickly raises and lowers the whole body on the spot, with a series of small jumps.

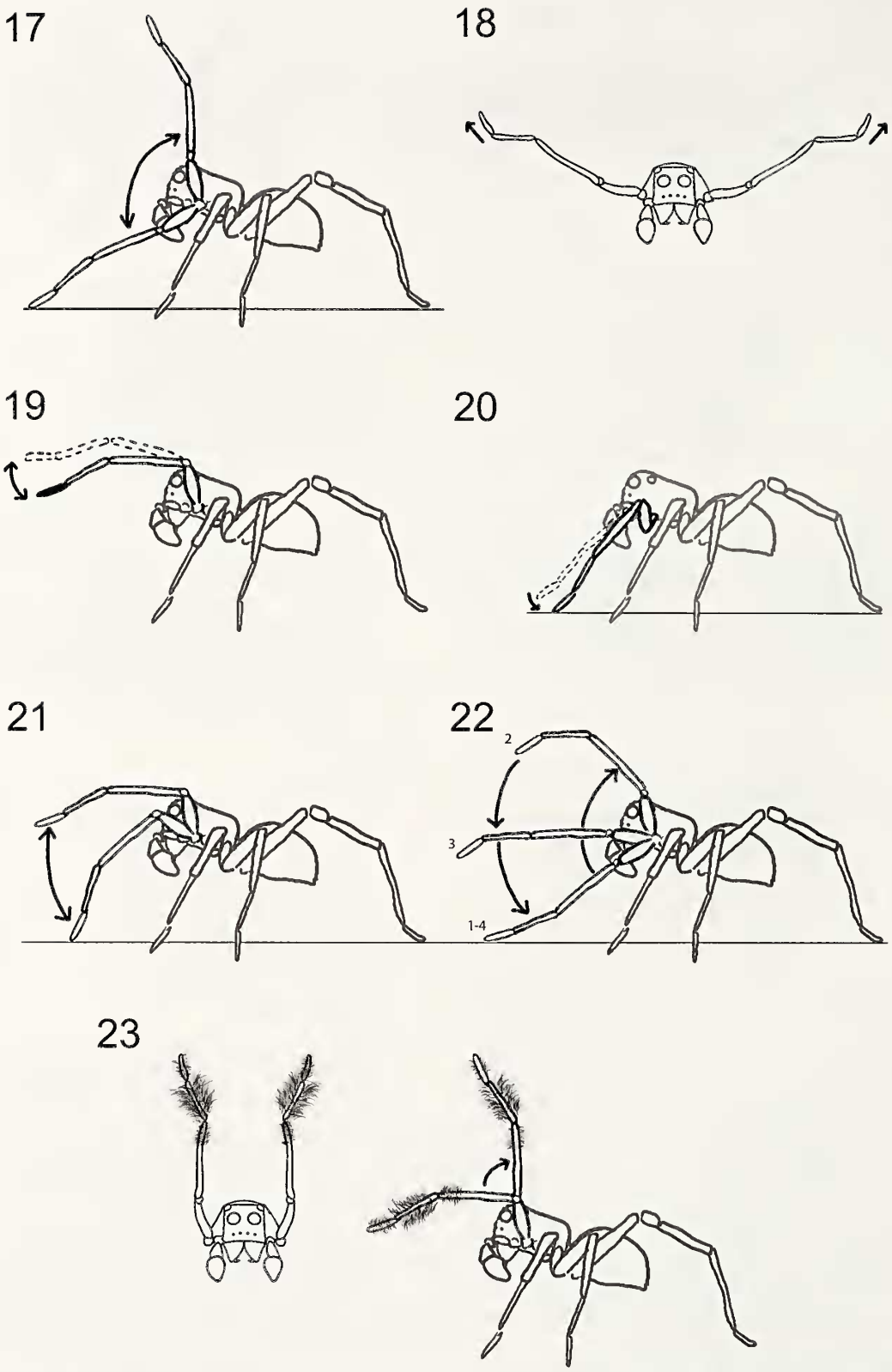
B_P, *pursuit*: the male pursues the female and gets closer. The chase ends when the female stops.

B_E, *encircling*: the male runs around the female, facing her and touching her legs.

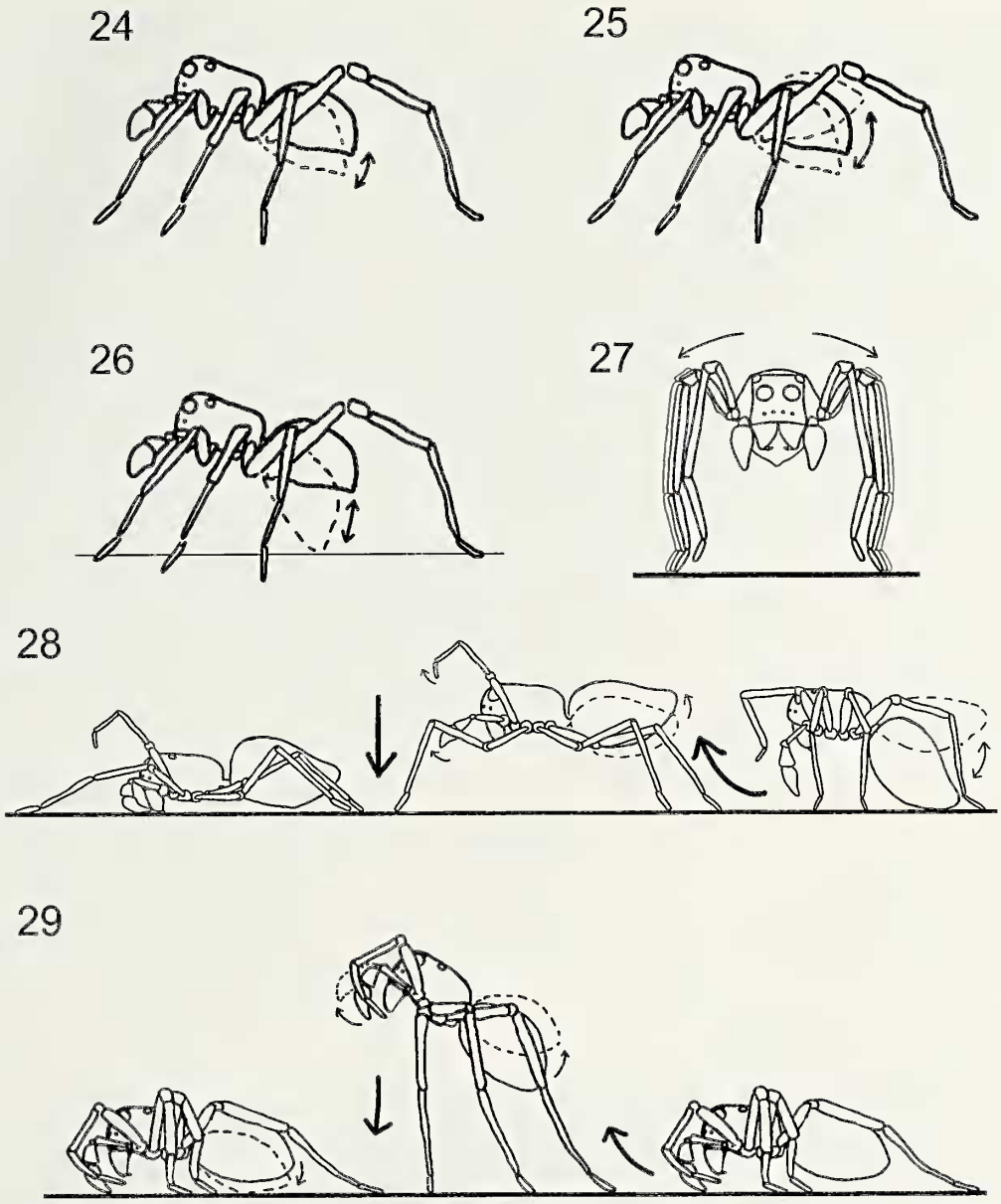
B_R, *retreat*: after contact with the female, a short backward run of the male, facing the female.

DESCRIPTION OF DISPLAYS

Species are listed according to Zyuzin's (1979) and Almquist's (2005) phenetic groups of species. For each group,



Figures 17–23.—Courtship elements in *Pardosa* species (forelegs). 17. Whipping (L_WH); 18. Lateral stretching/pumping (L_LS, L_P); 19. Oscillation (L_O); 20. Quivering (L_Q); 21. Tapping (L_T); 22. Waving (L_WA); 23. Raising (L_R, front and lateral views). See text for abbreviations.



Figures 24–29.—Courtship elements in *Pardosa* species (body and abdomen). 24. Twitching (A_TW); 25. Quivering (A_Q); 26. Tapping (A_TA); 27. Sideway waving (B_SW); 28. *P. prativaga* and *P. sphagnicola* hopping behavior (B_H); 29. *P. vlijmi* hopping behavior (B_H). See text for abbreviations.

we provide a brief introduction with taxonomical information concerning the species included in the group. For each species, we describe the average courtship display referring to the previous description of courtship elements. A list of materials examined (n = number of observed specimens) and a list of available literature on courtship are provided.

Pardosa amentata group

Only one European species is currently placed in the *P. amentata* group (Almquist 2005).

Pardosa amentata (Clerck 1757)

Material: ITALY: *Piedmont*, Province of Torino, Bobbio Pellice, Conca del Prà, alpine meadow (1732m a.s.l.), 9 November 2006, n = 5, A. Chiarle (MRSN); Province of Cuneo, Valdieri, alpine meadow (1763m a.s.l.), 4 April 2007, n = 6, A. Chiarle (MRSN). SWEDEN: *Uppland*, various localities in the vicinity of Stockholm, 1976–1982, n = 4, T. Kronestedt (NHRS).

Literature: Locket (1923), Bristowe & Locket (1926), Schmidt (1957), Bristowe (1958), Vlijm et al. (1963), Vlijm & Dijkstra (1966), Vlijm et al. (1970), Cordes (1995).

Description of the display: The male stretches out his palps with a fast movement (0.92 ± 0.18 sec, 101 observations, n = 5 individuals), one pointing obliquely upwards and forwards, the other obliquely downward and forward (P_SE). P_SE is then repeated after a few seconds (1.45 ± 0.41 sec, 49 observations, n = 5 individuals), reversing the position of the palps about three times (number of switching: 3 ± 1 times, 50 observations, n = 5 individuals). During P_SE the male performs A_TW, with an angle of about 45 °. Every time the palps switch their position, the male takes a step forward toward the female. While keeping the palps in this position, he

begins P_Q, together with L_Q and A_Q for about four seconds (4.03 ± 1.39 sec, 42 observations, n = 5 individuals), bringing them back to the starting position. Then the male repeats P_SE. The quivering of the first pair of legs results in a percussive signal, which was recorded by Cordes (1995).

Pardosa bifasciata group

The Palearctic *P. bifasciata* group is represented in Europe by two species: *P. bifasciata* and *P. schenkeli* (Zyuzin 1979).

Pardosa bifasciata (C.L. Koch 1834)

Material: BELGIUM: *Namur*, Viroinval, Nismes, sandy substrate (198m a.s.l.). 4 June 2009, n = 3, A. Chiarle (RBINS).

Literature: none.

Description of the display: The male alternates P_W and L_WA with slow movements touching the substrate. A series of about eight rapid stiff-legged hops toward the female (B_H, number of hops: 8 ± 4 times, 27 observations, n = 3 individuals; duration of a single hop: 0.23 ± 0.07 sec, 39 observations, n = 3 individuals) follows. At the same time, the male performs L_WH and P_Q.

Pardosa schenkeli Lessert 1904

Material: SWEDEN: *Dalarna*, Mora, pine forest on sand with *Cladonia* cover, patches with *Arctostaphylos uva-ursi* and bare sand, 26 May 1980, n = 2, T. Kronestedt (NHRS); Ore, Näset, similar habitat as previous, 23 May 1983, n = 1, T. Kronestedt (NHRS).

Literature: Kronestedt 2005.

Description of the display: The male starts with very rapid synchronous movements of the black palps with their tips pointing down (P_P). Rapid vertical bounces (B_B) of the body follow, and the palps continue to vibrate. During this behavior, performed on the spot, the distal part of the abdomen taps the substrate (A_TA) and performs rapid L_WH. The entire behavior is repeated after a short pause. Sounds from A_TA produced on substrate cardboard are illustrated in Fig. 51.

Pardosa lugubris group

The Palearctic species included in the *P. lugubris* group are morphologically almost identical, both in general appearance and genital organs. Furthermore, they can often be found in syntopy. The group was previously referred to as the *P. amentata* group (Zyuzin 1979), and only two European species were included in the group: *P. lugubris* and *P. amentata*. Töpfer-Hofmann et al. (2000) highlighted ethological differences within the group by comparing courtship behaviors and described two new species (*P. saltans* and *P. pertinax*). Moreover, they removed *P. amentata* from the *P. lugubris* group, both on behavioral and morphological bases. Kronestedt (1999) previously drew a similar conclusion on a morphological basis. At present, six species are listed for this group.

Courtship display in *Pardosa lugubris sensu lato* aroused the interest of several authors (Bristowe 1929; Vlijm & Dijkstra 1966; Hallander 1967; Vlček 1995; Töpfer-Hofmann et al. 2000). *Pardosa lugubris* shows a simple visual display: the male pursues the female (B_P) until she stops; and then he performs P_TC, L_LS, and A_TW while trying to mount her. In contrast, *Pardosa saltans* courtship behavior is rather complex and can be divided into several elements. Firstly, the male performs L_LS, P_TC, and A_TW and then starts to move the forelegs up and down (L_P) with low amplitude movements. At the same time, the palps are slowly raised alternately (P_SRL), and the abdomen twitches a few times (A_TW). After a few P_SRL, both palps are lowered slowly to the resting position. Immediately after, the male raises both palps (P_TRL) and runs in a circle around her (B_E). Given that only *P. lugubris* and *P. saltans* were filmed in the frame of this work, no other species belonging to this group were included in our analysis. In general terms, the other species belonging to this group (*P. alacris*, *P. baehrorum*, *P. caucasica* Ovtsharenko 1979, *P. pertinax*) perform slow motion palpal jerks and trembling in front of the female (for more details see Töpfer-Hofmann et al. 2000).

Pardosa monticola group

The *P. monticola* group is the largest group within the genus *Pardosa*, with 23 species occurring in Europe listed in Platnick's catalog (2012). Some of the species belonging to the *P. monticola* group are hardly distinguishable, especially the females. In contrast, males reveal some distinctive features allowing identification at the species level (Tongiorgi 1966b).

Several subspecies belonging to the *P. monticola* group have been described and eight of them [*P. agrestis purbeckensis* F.O.P.-Cambridge 1895, *P. agricola borussica* (Dahl 1908), *P. agricola fucicola* (Dahl 1908), *P. monticola ambigua* Simon 1937, *P. monticola minima* Simon 1876, *P. monticola pseudosaltuaria* Simon 1937, *P. palustris islandica* (Strand 1906), and *P. torrentum integra* Denis 1950] are considered valid (Platnick 2012). Most of the descriptions are generally based on phenetic characters, such as body and leg coloration.

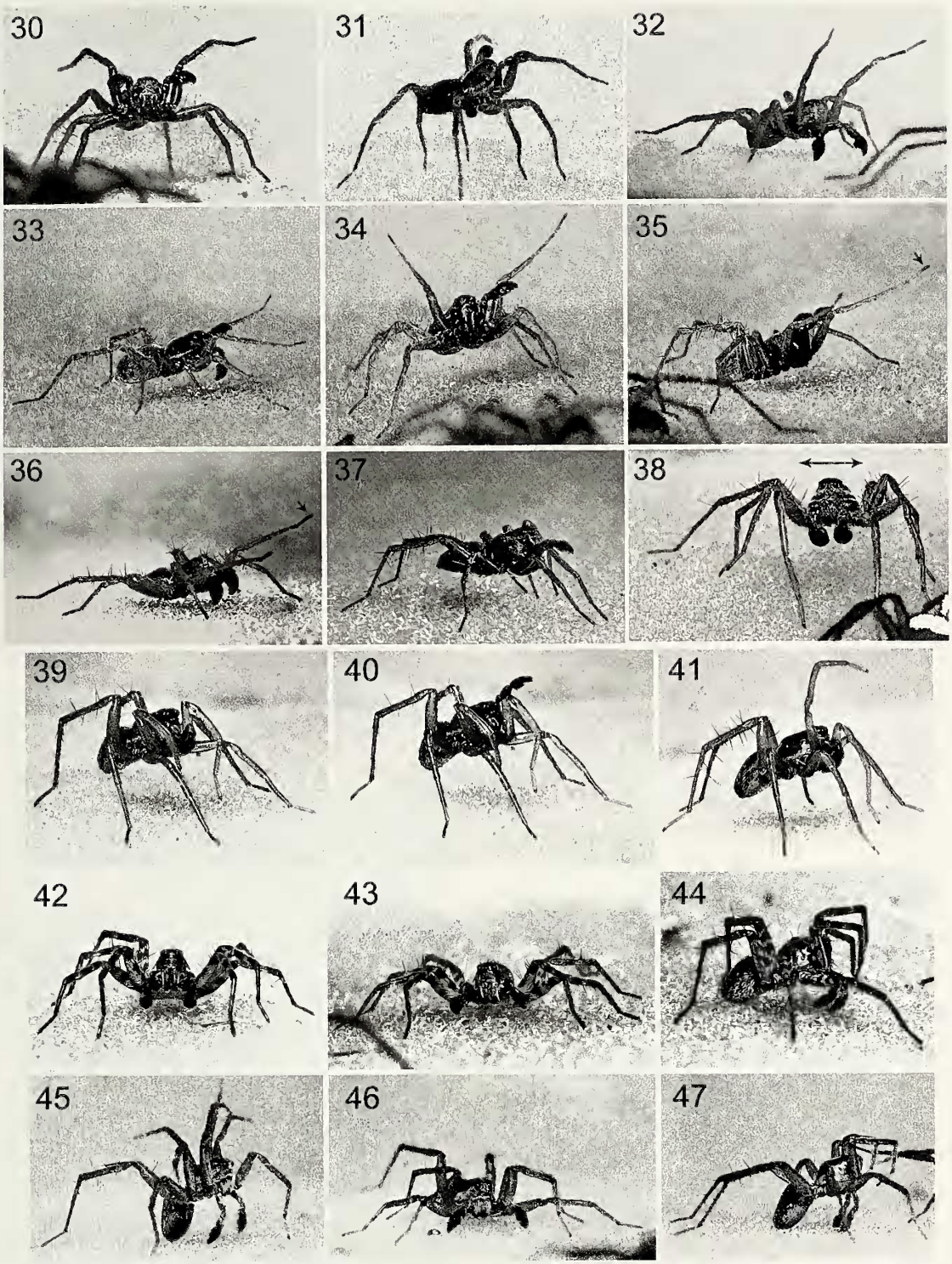
Among them, the taxonomic status of *P. agrestis purbeckensis* has been often debated. Currently, Platnick (2012) recognizes its validity in accordance with Alderweireldt & Maelfait (1993) and Pirchegger & Thaler (1999) who found no morphological differences in the male palp in order to support *P. purbeckensis* F.O.P-Cambridge 1895 as a valid species.

However, according to several authors (Knülle 1954; Tongiorgi 1966b; Heimer & Nentwig 1991), this hypothesis does not seem in accordance with other features such as differences in habitat preference (salt marshes and humid areas for *P. agrestis purbeckensis* versus meadows, arable lands and other open areas for *P. agrestis*) and morphological traits of the male forelegs. In addition, former descriptions of the courtship display (Bristowe 1929; Kronestedt 1979a) clearly support the elevation to species level.

Concerning the other species of this group, Kronestedt (1979a) described the courtship behavior of *P. agrestis*, *P. agricola*, *P. monticola* and *P. palustris* in a local Swedish journal. We provide the English description of the displays of these species and the first descriptions of the courtship behavior of *P. torrentum*, *P. blanda*, and *P. mixta* and provide further ethological evidence to support the elevation of *P. agrestis purbeckensis* to the species level.

Pardosa agrestis (Westring 1861)

Material: BELGIUM: *Brabant*, Tienen, sugar factory, sandy substrate (52m a.s.l.), 20 May 2009, n = 8, A. Chiarle,



Figures 30–47.—Male courtship postures in *Pardosa* species. 30–32. *P. purbeckensis*: 30–31. Palps and forelegs raised (P_SWR and L_R, frontal and posterior view); 32. Palps lowered and forelegs oscillating (L_O). 33–35. *P. agrestis*: 33–34. First legs moved slightly back and forth and palps jerkily raised in alternation or, sometimes, in synchrony (P_LWJ and L_O, lateral and frontal view); 35. L_O, arrow points at darkened tip of first tarsus; 36. *P. agricola*: L_O, arrow points at the mostly blackened tarsus. 37. *P. monticola*: palp raised (P_RL). 38. *P. palustris*: body slow sideways waving (B_SW). 39–41. *P. fulvipes*: 39. Initial posture with first legs raised; 40. Left palp raised (P_RL, cymbium pointing obliquely outwards); 41. Right first leg raised (L_WA, before straightened forwards and slowly lowered). 42–44. *P. prativaga*; 42. Initial position while performing few synchronous back and forth movements of the palps; 43. Rapid up and down movements of the obliquely outward directed palps (P_Q, tips directed downwards); 44. Close to female after a series of hops (B_H). 45–47. *P. sphagnicola*: 45. Elevated position during hopping behavior (B_H); 46. Low position during hopping behavior (B_H); 47. Close to female after a series of hops. (Photos T. Kronestedt). See text for abbreviations.

F. Hendrickx & J. Pétillon (RBINS). ITALY: *Piedmont*, province of Cuneo, Caraglio, Bottonasco, cultivated field (626m a.s.l.), 21 July 2007, $n = 5$, M. Isaia (MRSN). SWEDEN: *Uppland*, Stockholm, grassland, 1–3 June 1976, $n = 2$, T. Kronestedt (NHRS). Rådmansö, Gräddö, 2 June 1974, $n = 2$, T. Kronestedt (NHRS).

Literature: Kronestedt (1979a).

Description of the display: The male starts courting by alternately raising and lowering the palps while performing a series of about fourteen vertical movements of the cymbium (14 ± 3 times, 65 observations, $n = 5$ individuals; duration of one movement: 0.21 ± 0.02 sec, 36 observations, $n = 5$ individuals) drawing semi-circles with the palp (P_LWJ, Figs. 33–34). P_LWJ is performed by both palps alternately or, rarely, together. The forelegs are raised and moved slightly back and forth (L_O, Fig. 35), in synchrony with the movements of the palps (exposing the black tip of the tarsi) and the abdomen (AT_W). When the male stops performing P_LWJ, he steps toward the female (single step duration = 1.32 ± 0.30 sec, 36 observations, $n = 5$ individuals) and performs A_TW and L_Q. Then he starts P_LWJ, L_O and A_TW again.

Pardosa agricola (Thorell 1856)

Material: SWEDEN: *Dalarna*, Ore, lake Skattungen, sandy shore with reed debris, 1974–1979, $n = 5$, T. Kronestedt (NHRS).

Literature: Kronestedt (1979a).

Description of the display: The male starts waving the palps (P_W) in a down-flexed position, performing A_TW and L_O at the same time (Fig. 36). Forelegs are raised so that femora are directed upward and patellae-tarsi are directed forward, exposing the blackened tarsi. When approaching the female, the male moves his palps, tips directed towards the substrate.

Pardosa blanda (C.L. Koch 1833)

Material: ITALY, *Piedmont*, province of Cuneo, Acceglio, Sorgenti del Maira, alpine meadow (1566m a.s.l.), 2 June 2009, $n = 7$, M. Isaia (RBINS); province of Cuneo, Melle, Colle della Ciabra, alpine meadow (1723m a.s.l.), 24 May 2009, $n = 8$, M. Isaia (RBINS).

Literature: none.

Description of the display: The male follows the female, performing P_Q and A_Q (duration: 0.52 ± 0.21 sec, 34 observations, $n = 5$ individuals). When the female stops, the male performs about six hops (B_H, number of hops: 6 ± 4 times, 48 observations, $n = 5$ individuals) toward the female (duration of a single hop: 0.67 ± 0.23 sec, 76 observations, $n = 5$ individuals). B_H starts with a step forward toward the female with L_WH. Immediately after, the male performs about two (2 ± 1 times, 72 observations, $n = 5$ individuals) small steps with P_UDJ, L_T and A_TA. If the female runs away, the male lifts the prosoma, performing A_TW and P_W once.

Pardosa mixta (Kulczyński 1887)

Material: ITALY: *Piedmont*, province of Cuneo, Vernante, Palanfrè, alpine meadow (1340m a.s.l.), 30 June 2010, $n = 9$, A. Chiarle (RBINS).

Literature: none.

Description of the display: When the female is not moving, the male starts performing cautious B_SW movements toward her (duration of each wave: 1.53 ± 0.75 sec, 73 observations, $n = 5$ individuals). Getting closer to the female, the male performs L_R (duration: 0.20 ± 0.10 sec, 43 observations, $n = 5$ individuals). If the female remains on the spot, the male performs P_ARJ and after that suddenly leaps toward her, performing L_WH against her body (duration: 0.25 ± 0.05 sec, 57 observations, $n = 5$ individuals). Simultaneously, the male starts P_Q and A_TA. The legs are kept high, stretched almost perpendicular to the substrate, exhibiting the hairiness on the tarsus, metatarsus, and tibia. While keeping this position, the male starts P_ARJ and A_TW. If the female remains motionless, the male hits the female with L_WH. If the female runs away, the male repeats P_ARJ and A_TA, alternating it with B_SW until he reaches the female again.

Pardosa monticola (Clerck 1757)

Material: SWEDEN: *Uppland,* Runmarö, Vitträsk, 11 May 1974, $n = 1$, T. Kronestedt (NHRS); Vallentuna, Örsta, rock with lichens, 6 June 1976, $n = 3$, T. Kronestedt (NHRS); Bohuslän, Hamburgön, rocky habitat at the sea, 26 May 1979, $n = 1$, T. Kronestedt (NHRS).

Literature: Kronestedt (1979a).

Description of the display: The male remains still on the spot, performing a single abdominal twitch (A_TW) now and then. During A_TW, the male quickly raises one of the palps upward and forward (Fig. 37) and lowers it slowly (P_RL). After a few more A_TW, the male raises the other palp and slowly lowers it (P_RL). As an example, the time interval between each P_RL was 12, 15, 15, 21, and 47 sec. Finally, the male rapidly approaches the female.

Pardosa palustris (Linnaeus 1758)

Material: SWEDEN: *Uppland,* Vallentuna and Täby, May–June 1974–1979, $n = 4$, T. Kronestedt (NHRS); *Dalarna*, Ore, Näset, 25 June 1978, $n = 1$, T. Kronestedt (NHRS).

Literature: Kronestedt (1979a).

Description of the display: The male moves slowly toward the female performing B_SW (Fig. 38). At the same time he performs P_W in a down-flexed position and A_TW, now and then.

Pardosa purbeckensis F.O.P.-Cambridge 1895 **stat. rev.**

Material: NETHERLANDS: *Friesland*, Lauwerszeepolder, 30 April 1974, $n = 6$, T. Kronestedt (NHRS).

Literature: Bristowe (1929), Kronestedt (1979a).

Description of the display: The male starts courting by raising the palps synchronously in one to three jerky movements (tips of palps upwards and sideways) (P_SWR). The male then raises the forelegs (L_R) and directs them forward and upward, obliquely (Figs. 30, 31). The palps are then lowered in synchrony and moved up and down (tips directed downwards) while the front legs, directed forward, oscillate rapidly (L_O) (Fig. 32). Abdominal twitching may occur (A_TW). The movements are performed on the spot, and sometimes the male leans his body forward toward the female. The entire sequence may be repeated several times.

Based on these observations and from arguments given above, we propose the re-establishment of *P. purbeckensis* as a distinct species.

Pardosa torrentum Simon 1876

Material: ITALY: *Piedmont*, province of Verbania Cusio Ossola, Fondo Toce – Riserva Naturale Speciale di Fondo

Toce, artificial lake shore (193m a.s.l.), 6 April 2009, $n = 10$, A. Chiarle & M. Paschetta (RBINS).

Literature: none.

Description of the display: When the male approaches the female, he starts A_TW, followed almost immediately by A_TA. This behavior turns into B_SW (number of consecutive oscillations: 21 ± 16 times; duration of a single oscillation: 0.40 ± 0.12 sec, 89 observations, $n = 5$ individuals) with L_O. The legs are raised obliquely and slowly and rhythmically oscillated. At the same time, the palps (down-flexed at the beginning) are moved up and down, keeping them in contact with the substrate (P_UDJ). While performing these movements, the male slowly approaches the female.

Pardosa nigra group

The *P. nigra* group has a Holarctic distribution and is morphologically distinct from other *Pardosa* species in having the male palp with tegulum strongly protruding ventral and a terminal apophysis characteristically connected to the palea. (Tongiorgi 1966a; Lowrie & Dondale 1981; Kronestedt 2004). Five species occur in Europe: *P. eiseni* (Thorell 1875), *P. giebeli* (Pavesi 1873), *P. lasciva* L. Koch 1879, *P. nigra* (C.L. Koch 1834) and *P. trailli* (F.O.P.-Cambridge 1873). This is the first account of courtship behavior in a species of this group.

Pardosa nigra (C.L. Koch 1834)

Material: ITALY: *Piedmont*, province of Torino, Mompantero, Rocciamelone, Alpine scree (3538m a.s.l.), 30 June 2007, $n = 5$, M. Isaia (MRSN).

Literature: none.

Description of the display: The male bends his body at the pedicel and performs P_C (duration: 0.38 ± 0.24 sec, 75 observations, $n = 5$ individuals) continuously, tips directed downward. At the same time, he performs L_R. These movements occur on the spot. After about three P_C (3 ± 2 times, 60 observations, $n = 5$ individuals), the male performs B_H and L_WH toward the female (duration of a single hop: 0.40 ± 0.10 sec, 100 observations, $n = 5$ individuals). At the end of each B_H, the male again starts P_C on the spot.

Pardosa nigriceps group

The *P. nigriceps* group encompasses two species (Hippa & Mannila 1982), both occurring in Europe: *Pardosa maisa* Hippa & Mannila 1982 and *P. nigriceps* (Thorell 1856). The courtship behavior of *P. nigriceps* has already been described in the literature, but no description is available for *Pardosa maisa*.

Pardosa nigriceps (Thorell 1856)

Material: BELGIUM: *Namur*, Viroinval, Nismes, meadow, 7 June 2009, $n = 10$, F. Hendrickx (RBINS). SWEDEN: *Uppland*, Täby, 10 May 1983, $n = 2$, T. Kronestedt (NHRS).

Literature: Locket (1923), Bristowe & Locket (1926), Bristowe (1958), Vlijm & Dijkstra (1966).

Description of the display: The male starts with slow movements toward the female with cautious steps and performing continuous palpal cycling (P_CC) (10 ± 8 times in one courtship session; one P_CC duration: 2.80 ± 1.05 sec, 73 observations, $n = 5$ individuals) and abdominal twitching (A_TW). When he gets closer to the female, he performs L_Q.

Pardosa proxima group

According to Zyuzin (1979), the *P. proxima* group comprises eight species, all confined to the Palearctic region. *Pardosa proxima* was originally described from Greece (Koch 1847). This species is widespread in open habitats in the Mediterranean basin (Den Hollander & Dijkstra 1974). The individual variability of *P. proxima* is very high, even within the same population, both in genital structures and general morphology (Tongiorgi 1966a). One subspecies, *P. p. poetica* Simon 1876, is still considered valid though, according to Tongiorgi (1966a); the validity of subspecies of *P. proxima* needs reconsideration. The first observations of the courtship behavior of *P. proxima* were given in Den Hollander et al. (1972). In the same work *P. vlijmi* was described as a new "ethospecies" from France. According to Den Hollander & Dijkstra (1974) and confirmed by our findings; *P. proxima*, *P. vlijmi*, and *P. hortensis* may occur in syntopy.

Pardosa hortensis (Thorell 1872)

Material: ITALY: *Piedmont*, province of Cuneo, Guarene, Sotteri, meadow (155m a.s.l.), 7 March 2009, $n = 8$, A. Chiarle (RBINS); province of Cuneo, Diano d'Alba, Gaiole Rinaldi, vineyard (275m a.s.l.), 9 July 2007, $n = 5$, A. Chiarle (MRSN).

Literature: Vlijm & Dijkstra (1966).

Description of the display: The male starts P_SC (number of steps: 4 ± 1 times each semicircular movement; one step duration: 0.78 ± 0.61 sec, 70 observations, $n = 5$ individuals; one P_SC duration: 4.08 ± 1.61 sec, 35 observations, $n = 5$ individuals). During P_SC, the male also performs L_Q, while stepping cautiously toward the females. Sporadic A_TW may occur.

Pardosa proxima (C.L. Koch 1847)

Material: ITALY: *Piedmont*, province of Cuneo, Guarene, Sotteri, meadow (155m a.s.l.), 22 March 2009, $n = 11$, A. Chiarle (RBINS).

Literature: Den Hollander & Dijkstra (1974), Chiarle & Isaia (2013).

Description of the display: The male moves a step forward (step duration: 0.39 ± 0.12 sec, 40 observations, $n = 6$ individuals) while performing L_R, P_W and A_TW. The male then moves toward the female with hops (B_H, mean number of hops = 5 ± 3 times; B_H, duration of single hop: 1.44 ± 0.35 sec, 215 observations, $n = 6$ individuals), while performing L_T, P_CR and A_TW. If the female runs away, the male raises its body and performs P_CR.

Pardosa vlijmi Den Hollander & Dijkstra 1974

Material: ITALY, *Piedmont*, province of Cuneo, Vicoforte Mondovì, Ermetta, meadow (534m a.s.l.), 07 March 2009, $n = 2$, A. Chiarle (RBINS); Guarene, Sotteri, meadow (155m a.s.l.), 22 March 2009, $n = 5$, A. Chiarle (RBINS).

Literature: Den Hollander & Dijkstra (1974), Chiarle & Isaia (2013).

Description of the display: The male starts B_B. The vibration turns into a conspicuous B_H, characterized by up and down movements of the whole body toward the female (mean number of hops: 9 ± 3 times; single hop duration: 0.60 ± 0.18 sec, 202 observations, $n = 6$ individuals). More specifically, the cephalothorax is raised due to the movements

of the posterior legs (second, third and fourth pairs), the first pair held near the body, parallel to the palps. At the same time, the male performs A_TW. In between B_H, palps and abdomen touch the substrate (P_CR and A_TA). If the female runs away, the male raises its body and performs P_CR.

Pardosa pullata group

The *P. pullata* group includes eight species and one subspecies, all found in the Palearctic region (Kronestedt 2007). The monophyly of this group is supported by morphology (division of the tegular apophysis into two membranously connected sclerites), as well as by molecular data (Zehethofer & Sturmbauer 1998; Goodacre & Kronestedt unpublished data). Some species have at times been treated as subspecies. Following Platnick (2012), only *P. prativaga scoparia* Simon 1937, reported from France, is still eonsidered valid.

Regarding courtship behavior, the *P. pullata* group is one of the most studied. Precopulatory behavior in *P. pullata* has been the subject for several studies (Bristowe & Locket 1926; Vlijm & Borsje 1969; Hallander 1967; Den Hollander 1971; Den Hollander al. 1973; Kronestedt 1979a, 2007). The different descriptions are congruent with each other, illustrating an inconspicuous visual display: the male rapidly jumps onto the female (B_J) and clasps her with its legs.

The behavior of *P. pyrenaica*, observed by Kronestedt (2007), is very similar to that of *P. pullata*, but, in addition, after the contact with the female, the male performs some alternating P_W. *Pardosa prativaga* and *P. sphagnicola* have been studied extensively by Den Hollander (1971: *P. prativaga fulvipes* = *P. sphagnicola*), Den Hollander et al. (1973) and Kronestedt (1979a).

Pardosa fulvipes (Collett 1876)

Material: SWEDEN: *Dalarna*, Ore, grassland, 3 June 1973, $n = 1$, T. Kronestedt (NHRS); *Uppland*, various localities in the vicinity of Stockholm, grasslands with thick cover of last year's grass debris, some adjacent to lakes, 1972–1987, $n = >20$, T. Kronestedt (NHRS).

Literature: Kronestedt (1979a).

Description of the display: The male initially takes up a posture with the first legs lifted up and hanging in front (Fig. 39). The two palps are then raised and lowered in alternation a few times (P_RL, duration of one palpal raising-lowering: 1.20 ± 0.10 sec, 10 observations, $n = 3$ individuals) (Fig. 40). This is followed by the raising and slowly lowering of the foreleg on the same side as the last lowered palp (L_WA, duration of one leg waving: 9.20 ± 1.20 sec, 12 observations, $n = 3$ individuals) (Fig. 41). During lowering, the leg is slowly waved with very slight bendings at the tibio-metatarsal joint. The thin hairs on the metatarsus are exposed during L_WA. When the foreleg touches the substrate, the body may jerk slightly and the palp on the opposite side is raised and lowered, followed by L_WA on the same side. During the display, the male performs small vertical twitches of the abdomen (A_TW), generating vibratory sensations from a paired stridulatory apparatus, barely heard by human ear when performed on an artificial substrate like cardboard (Kronestedt 1973).

Pardosa prativaga (L. Koch 1870)

Material: ITALY: *Piedmont*, province of Cuneo, Vicoforte Mondovì, Ermetta, meadow (534m a.s.l.), 21 March 2007, $n = 7$, A. Chiarle (MRSN). SWEDEN: *Uppland*, various localities in the vicinity of Stockholm, lake shores and adjacent grasslands, 1972–1983, $n = >25$, T. Kronestedt (NHRS).

Literature: Den Hollander et al. (1973), Kronestedt (1979a).

Description of the display: The male lowers its body, almost touching the substrate, then starts to vibrate the abdomen up and down (A_TA). This is very shortly followed by a few synchronous movements of the palps accompany the vibration. During this movement, the palps are held in a low position with their tips directed backward under the body (Fig. 42). After the very first vibrations, the abdomen taps on the substrate about 10 times (number of taps in one sequence: 10 ± 1 times, 20 observations; duration of one sequence with 10 taps: 1.76 ± 0.09 sec, 12 observations; interval between taps: 0.22 ± 0.01 sec, 96 observations, first shorter and weaker taps in a sequence not included; $n = 5$ individuals). This is followed by rapid synchronous up and down movements of the palps, cymbia now being directed downwards (P_Q) (duration of P_Q: 2.82 ± 0.48 sec, 87 observations, $n = 5$ individuals, Fig. 43). During the latter movements, the eymbia barely reach the substrate. This is usually followed by repeating A_TA with P_CR and P_Q a number of times until the male approaches the female in a series of B_H. During such hops, the male may perform A_TA and P_CR (number of hops varies according to the receptivity of the female, up to about 40 taps/hops have been recorded; interval between taps: 0.19 ± 0.02 sec, 130 observations, $n = 5$ individuals). Hops cease when the male is close to the female. Then the male approaches the female with raised first legs, tibiae parallel to the substrate and metatarsi perpendieular to the tibiae (Fig. 44). If the female moves away, the male quickly moves backward (B_R) (duration: 0.94 ± 0.27 sec, 32 observations, $n = 5$ individuals), performing a few abdominal taps. The whole behavior is repeated several times until copulation. Before starting a sequence, the male may approach the female and quickly touch her, then move baekwards (B_R) and perform encircling (B_E) (duration = 3.35 ± 1.39 see, 23 observations, $n = 5$ individuals). Sounds from A_TA produced on cardboard as substrate are illustrated in Fig. 48.

Pardosa riparia (C.L. Koch 1833)

Material: SWEDEN: *Dalarna*, Ore, various grasslands, 1977–1987, $n = 10$, T. Kronestedt (NHRS).

Literature: Kronestedt (1979a).

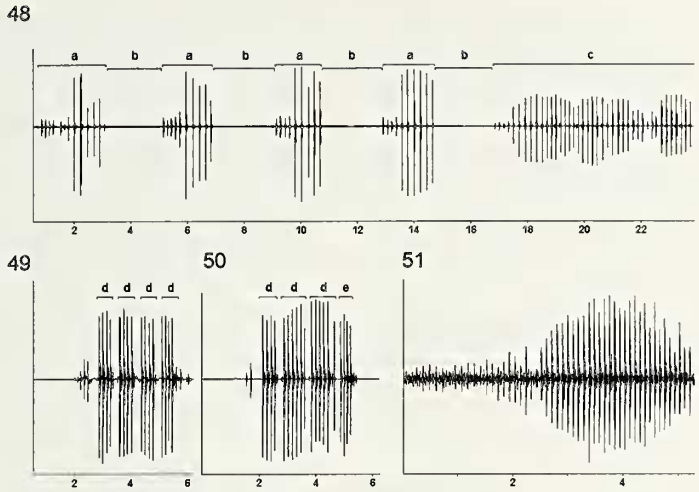
Description of display: There is no stereotypic visual component in the courtship. The male performs B_P intensely and tries to mount the female after a more or less intense struggle. When losing contact with the female, the male performs P_W and A_TW.

Pardosa sphagnicola (Dahl 1908)

Material: SWEDEN: *Dalarna*, Ore, various places, mires with *Sphagnum*, 1973–1981, $n = 5$, T. Kronestedt (NHRS); *Uppland*, various places in the vicinity of Stockholm, mires with *Sphagnum*, 1972–1983, $n = 13$, T. Kronestedt (NHRS).

Literature: Den Hollander et al. (1971: sub *P. prativaga fulvipes*, 1973), Kronestedt (1979a).

Description of the display: The male starts courting by performing vertical movements of the abdomen (A_TW) and synchronous movements of the palps, tips bent backward close



Figures 48–51.—Oscillograms illustrating the sound produced by abdominal tapping on cardboard during courtship in *Pardosa* species (time scale in seconds). 48. *P. prativaga*: sequence of four tapping groups (a) followed by tapping during hops towards female (c). Rapid up and down jerks of the palps (with no recorded acoustic effect: (b) are performed between each group of abdominal tapping. (a) and (b) are performed on the same spot; 49–50. *P. sphagnicola*: 49. Hopping sequence of four abdominal tapping groups (d) performed during approach towards female; 50. Hopping sequence of three abdominal tapping groups (d) performed during approach towards female and one group during retreat (e); 51. *P. schenkeli*: single abdominal drumroll (out of several) (51. from Kronestedt 2005).

to the body (P_Q). These movements increase in intensity, leading to a series of rapid hops (B_H, Figs. 45, 46), during which abdomen and forelegs tap the substrate (A_TA and L_T), and palps are held low with cymbia reaching the substrate (P_CR). B_H are fast and often grouped in about two to four (number of taps/hops in a sequence: 3 ± 1 times, 40 observations; time interval between taps/hops: 0.15 ± 0.02 see, 92 observations, $n = 6$ individuals), separated by a short break (time interval between tapping sequences: 0.32 ± 0.06 sec, 30 observations, $n = 6$ individuals). Hops cease when the male is close to the female and approaches her with first legs raised, tibiae being held parallel to the substrate and metatarsi perpendicular to the tibiae (Fig. 47). If the female runs away, the male quickly moves backwards (B_R) with A_TA and repeats the entire sequenee. Sounds from A_TA produced on cardboard are illustrated in Figs. 49, 50.

Pardosa wagleri group

Four species belonging to this group (Zyuzin 1979) occur in Europe, but only the courtship behavior of *P. wagleri* and *P. saturatior*, both occurring in riverine habitats, has been studied. *Pardosa wagleri* is widely distributed in low altitude riverbanks, while *P. saturatior* is restricted to higher altitudes (Tongiorgi 1966a). Despite the great similarity of the genitalia, Tongiorgi (1966a) separated these two species on ecological, phenological, and morphological basis. Barthel & von Helversen (1990) confirmed Tongiorgi's (1966a) observations, adding preliminary information on differences in courtship behavior.

Chiarle et al. (2010) described and compared the courtship behavior of *P. wagleri* and *P. saturatior*. In both species, jerky movements of the palps (P_LJ for *P. wagleri* and P_Q for *P. saturatior*) characterize the first part of the behavior, while performing L_WH, A_Q and A_TA. The male then starts B_P while performing all previous behaviors. *Pardosa saturatior* exhibits faster and more intense movements in its behavior than *P. wagleri*. The last part of the behavior, however, is identical, characterized by P_RL.

GENERAL CONSIDERATIONS

Movements mainly involving three body parts eharacterize courtship display in the genus *Pardosa*: the palps, the first pair of legs, and the abdomen. The most complex movements are performed by the palps, involving all joints in different movements. Legs are mainly oscillated in the air or vibrated on the substrate, while the abdomen is generally moved up and down with different speeds and amplitudes.

A considerable diversity in visual signaling behavior is shown both within and among the so-called "phenetic groups." Even if they do not refleet real phylogenetic groups, species-groups are still widely used for practical purposes in arachnological literature (Zyuzin 1979; Almquist 2005).

Despite strong morphological similarities in genitalia and habitus, species belonging to the *P. monticola* group show clear qualitative differences in courtship behavior. The general body movement of *P. blanda* is quite different from all the other species in the group, characterized by the male's hop-like movements towards the female. In contrast, *P. torrentum*, *P. mixta,* and *P. palustris* perform B_SW, while the other species display on-the-spot movements or move slowly toward the female. The movements of the palps are complex in all the species that we analyzed, especially in *P. agrestis*, *P. purbeckensis*, *P. mixta,* and *P. agricola*. The position of the front legs during the display is similar in *P. agrestis*, *P. torrentum* and *P. agricola*. It is worth noticing that the coloration of the tarsal forelegs may be related to such behavior, playing a role in the visual signal associated with the movements. Similarly, some other epigamic or amplifying traits in this group are found in the divergent hairiness on foreleg tarsi and metatarsi of *P. purbeckensis* and *P. mixta*, the latter lifting the forelegs high, exhibiting the hairiness on its metatarsi and tarsi to the female. As observed in the genus

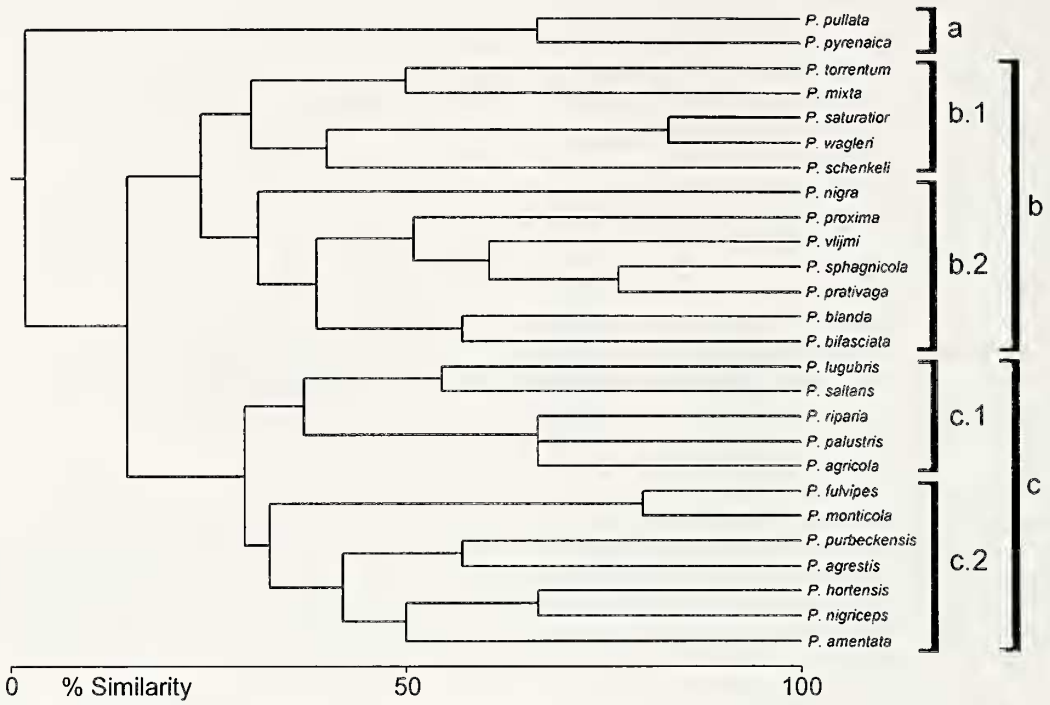


Figure 52.—Cluster analysis showing the degree of association within the species of *Pardosa* here considered (presence/absence data, group average link rule, Bray Curtis distance). Letters indicate groups discussed in the text.

Schizocosa, dark forelegs and tufts of hairs on the legs generally represent amplifying traits related to male qualities (McClintock & Uetz 1996; Scheffer et al. 1996; Hebets & Uetz 1999, 2000).

Among the species of the *P. pullata* group, the display of *P. fulvipes* (P_RL, L_WA and A_TW) shows no similarities to any other species of the group. Moreover, *P. fulvipes* uses a specific and unique stridulatory organ on the abdomen: the hairless striated surface of the book-lung opercula serves as the file, while the stout denticulated hairs on the fourth coxae form the scraper part (Kronestedt 1973). Despite the general complexity of the display observed in this group, three species show inconspicuous behaviors: *P. pullata*, *P. pyrenaica* and *P. riparia* simply jump on or chase the female (B_J and B_P). The elosely related *P. prativaga* and *P. sphagnicola* show comparable behaviors, with the presence of common traits: in both species the male approaches the female with a series of hop-like movements (B_H), characterized by tapping of the abdomen (A_TA) against the substrate, thus producing a percussive sound (Figs. 48–50).

Similar considerations can be drawn for the *P. proxima* group, in which the cryptic species *P. proxima* and *P. vlijmi* perform different behaviors. However, several hypothetical homologies, such as the general courtship patterns, B_H and P_CR are easily identifiable. *Pardosa hortensis*, belonging to the same group, performs P_SC, L_Q and A_TW, in contrast to the fast B_H in *P. proxima* and *P. vlijmi*.

Concerning the *P. wagleri* and *P. lugubris* groups, extensive and quantitative data are reported in Chiarle et al. (2010) and Töpfer-Hofmann et al. (2000) respectively. We refer to those works for the detailed description of the courtship displays. It is worth noticing that the presence of an identical ending behavior (P_RL) in *P. wagleri* and *P. saturatior* can be interpreted as a homology. Similarly, *P. lugubris* and *P. saltans*, though performing dissimilar behavior, share some identical CEs (L_LS and L_P).

COMPARATIVE ANALYSIS

Despite the fact that all categorizations are naturally subject to personal interpretation, we explored the degree of association between the European species of the genus *Pardosa* using a cluster analysis. The dataset was set up on the basis of the CEs previously described. We used the Bray-Curtis distance (group average link rule) to evaluate similarities among species and clustered them according to presence/absence of CEs within the display. The final matrix was thus composed of 35 lines (CEs) and 26 columns (species).

Pardosa prativaga, *P. sphagnicola*, and *P. blanda* show the highest number of CEs within the display (n = 9) followed by *P. mixta*, *P. sphagnicola*, and *P. saltans* (n = 7). *Pardosa pullata* (n = 1), *P. pyrenaica*, and *P. monticola* (n = 2) show the poorest displays in terms of the number of behavioral elements. A_TW (n = 18), A_TA (n = 9), and B_H (n = 7) and P_W (n = 7) had the most frequent CEs among the species. In general, palpal movements resulted in highly species-specific behaviors (P_SE, P_C, P_LWJ, P_P, P_ARJ, P_SWR, P_LJ, P_SRL, P_TRL, P_SC, P_CC). A similar trend occurred for leg movements such as L_P and L_LS (characteristic only of the *P. lugubris* group) and peculiar body movements such as B_R (shared by the two closely related species *P. sphagnicola* and *P. prativaga*) and B_J (shared by the two closely related species *P. pullata* and *P. pyrenaica*).

The cluster analysis (Fig. 52) highlights the partitioning of the species in three main clusters, based on the presence of different CEs within the displays. Group "a" is composed of two species (*P. pullata* and *P. pyrenaica*) performing simple visual displays characterized by one or two CEs (P_W and

B_J). Group "b" is characterized by species performing rapid, directional movements toward the female (B_H, B_B, B_P, B_R, B_E). This cluster could be further subdivided into two subgroups. The first subgroup (b.1) is composed of three species (*P. wagleri*, *P. saturatior*, and *P. schenkeli*) that perform relatively fast movements of the palps (P_Q, P_P, P_RL, P_LJ), while the legs are whipped (L_WH) and the abdomen is quivered (A_Q) or tapped (A_TA) against the substrate. The second sub-cluster (b.2) includes seven species (*P. nigra*, *P. proxima*, *P. vlijmi*, *P. sphagnicola*, *P. prativaga*, *P. blanda*, and *P. bifasciata*), which perform hopping behavior (B_H). Palpal movements within this subgroup are mainly characterized by quivering (P_Q) or waving (P_W). In addition, cymbium rubbing (P_CR) may occur. Group "c" encompasses all the remaining speeies, and in this case two subgroups can be highlighted. The first subgroup (c.1) comprises the two closely related species *P. lugubris* and *P. saltans*, three species of the *P. monticola* group (*P. agricola*, *P. monticola*, and *P. palustris*) and two species of the *P. pullata* group (*P. fulvipes* and *P. riparia*). This cluster is rather heterogeneous, and thus no clear characteristics can be highlighted. In general, the displays are predominantly slow and cautious, with faster final stages. The last subgroup (c.2) encompasses seven species (*P. agrestis*, *P. amentata*, *P. hortensis*, *P. mixta*, *P. nigriceps*, *P. purbeckensis* and *P. torrentum*), whose males generally court on the spot or approach the female with small steps. The movements of the palps are, however, highly species-specific, characterized by up and down movements (P_UDJ, P_SWR, P_Q) and semi-circular movements (P_ARJ, P_LWJ, P_SE, P_SC, P_CC). Leg quivering (L_Q) and leg oscillation (L_O) is generally associated with the movement of palps while the abdomen is twitched (A_TW), occasionally during the whole courtship. Only *P. mixta* and *P. torrentum* perform abdomen tapping (A_TA).

Aecording to our analysis, the species do not show high levels of similarity due to the species-specificity of each courtship display. However, it is possible to highlight some hypothetical homologies in certain closely related species. Some examples are provided by *P. torrentum*, *P. palustris*, and *P. mixta* (B_SW), *P. sphagnicola* and *P. prativaga* (shared CEs: P_Q, P_CR, A_TA, B_H), *P. saturatior* and *P. wagleri* (shared CEs: P_RL, L_WH, A_TA, A_Q, B_P), *P. pullata* and *P. pyrenaica* (shared CEs: B_J, unique for these two species) and *P. lugubris* and *P. saltans* (shared CEs: P_TC, A_TW, L_LS). As reported by Vlijm & Dijkstra (1966), it is interesting to note that *Pardosa hortensis*, *P. nigriceps* and *P. amentata* all belong to different morphological species groups, but show very similar courtship outlines.

CONCLUSIONS

Almost all the species that we observed showed a high level of complexity, both in terms of sensory modes involved and number of CEs comprising the display. A similar level of complexity was observed in some other lycosids (Stratton & Uetz 1983; Scheffer et al. 1996). As stated by Bull (1979) regarding the complex courtship of the grasshopper *Myrmeleotettix maculatus*, complexity in visual display might have arisen due to different mechanisms sueh as 1) an increase in male attractiveness in a heterogeneous environment; 2) reproductive isolation between closely related species upon seeondary contact; 3) sexual selection if males with higher display complexity have a greater fitness; and 4) sensory exploitation and female preference for complexity. Moreover, the organization of courtship is hierarchical, and it is possible to split the behavior into different semi-independent parts regarding their regulation, function and evolution. All of these features facilitate independent variation of different CEs, increasing diversification and complexity. Despite the observed general complexity, in five out of the nine groups studied in this work, we found species with simple courtship behavior: *P. pullata*, *P. pyrenaica*, *P. riparia*, *P. lugubris*, *P. bifasciata* and *P. nigra*. If conspicuous traits lose their previous importance, selection should act by reducing costly courtship display regarding both energy expenses and conspicuousness to rival males or other predators (Bull 1979).

In conclusion, courtship behavior in genus *Pardosa* is very diversified, and in several cases it is hard to reconstruct the path that leads to a particular courtship within the same morphology-based species group. Furthermore, it is also possible to find similar or identical behavior in species that are not closely related, such as the hopping behavior in both *P. proxima* (*P. proxima* group) and *P. blanda* (*P. monticola* group) or the elliptical movements of the palps in *P. hortensis* (*P. proxima* group) and *P. nigriceps* (*P. nigriceps* group).

For these reasons, the study of eourtship behavior represents a useful tool for identifying cryptic species due to the qualitative differences that can be observed in closely related species (see Den Hollander & Dijkstra 1974 and Töpfer-Hofmann et al. 2000). However, courtship behavior should not be used solely to infer phylogenetie relationships among species as highlighted by the cluster analysis.

Further studies on this topic are thus needed to increase the knowledge of both the biology of *Pardosa* species and the evolution of such complex behaviors. In parallel with the genus *Schizocosa* (see McClintock & Uetz 1996; Scheffer et al. 1996; Hebets & Uetz 1999, 2000; Uetz 2000; Taylor et al. 2005; Delaney et al. 2007; Gibson & Uetz 2008; Vaccaro et al. 2010), *Pardosa* models may provide useful tools to study the evolution of communication and behavioral complexity.

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